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Rhodora

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CONTRIBUTIONS FROM THE GRAY HERBARIUM OF HARVARD UNIVERSITY.—NO. XCIII

SPECIFIC SEGREGATIONS AND IDENTITIES IN SOME FLORAS OF EASTERN NORTH AMERICA AND THE OLD WORLD[1]

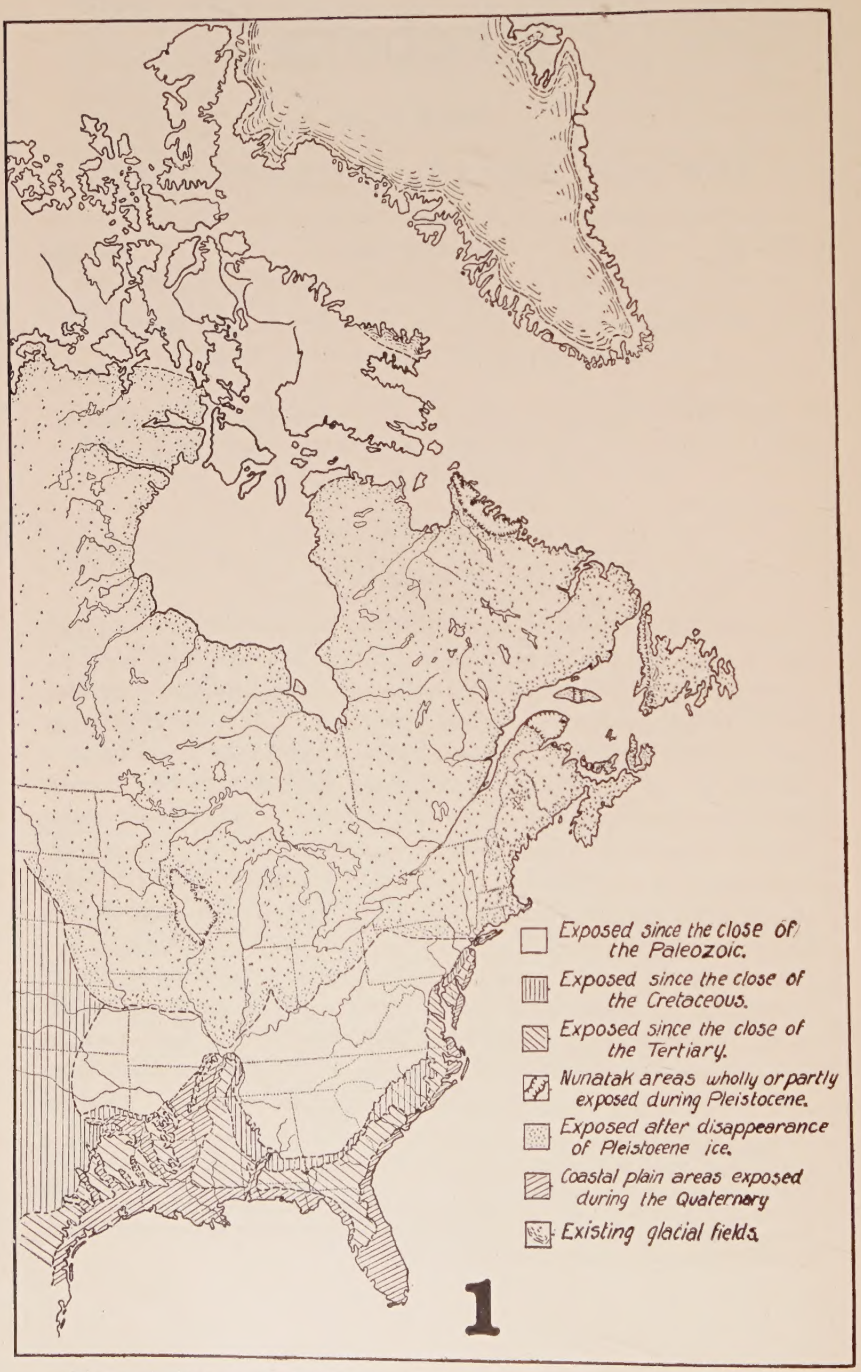
M. L. Fernald

(Plate 204)

I have assumed that I am expected to base my discussion primarily on some features of phytogeography which I have personally examined, rather than to attempt extensive generalizations concerning floras with which I am absolutely unfamiliar. Granted this assumption, I must start with a consideration of problems centering on a limited area of eastern North America, the region of the Atlantic slope extending from the Labrador Peninsula to the Atlantic States and the Mississippi Valley (map 1). This district, however, is sufficiently extensive clearly to exhibit large areas which, since the dawn of Angiosperms, have had quite different physiographic and floristic histories.

Viewed from the standpoint of availability for occupation by flowering plants, the oldest large section of the region is the southern half of the Appalachian Upland, extending from central New York to northern Georgia and northern Alabama, and west of the Mississippi represented by the Ozark Plateau. Never, since it was first occupied

[1] Originally announced under the above title for the joint Discussion on *Geographical Distribution and its Relation to the Concept of Species* of Sections E (Phytogeography and Ecology) and T (Taxonomy and Nomenclature) but, at the invitation of the Executive Committee, expanded and presented (under an abbreviated title) in the General Programme of the Fifth International Botanical Congress at Cambridge, England, Thursday evening, August 21, 1930.



Map 1, Periods of Availability for Plant-Occupation of Eastern North America since the Paleozoic.

by Angiosperms, has the Appalachian Upland of the United States (and Canada) been invaded by seas; and, except for its northern extension, it lies wholly south of the limits of the Pleistocene glaciation. During the Cretaceous, while this southern half of the Appalachian region was covered by land-vegetation, the lower marginal country, east, south and far to the west and northwest, was submerged under the Cretaceous seas. In the Tertiary, likewise, much of the low-lying Coastal Plain was again covered by shallow seas; and, furthermore, the outer margin of the Coastal Plain is often of very modern or Quaternary origin.

North of the southern Appalachians and extending north to northern Labrador and the subarctic and arctic continental coast is the area which was covered by Pleistocene ice, the last advance of which, the Wisconsin, is estimated to have begun its frontal decay only 25,000-30,000 years ago, while the northern limit of this advance in eastern America is represented by the living glacial field of eastern Baffin Island and the almost continental ice-cap of Greenland. Although the Wisconsin or most recent continental ice-sheet in the median latitudes of North America and its confluent valley-glaciers together denuded or modified a vast area, there are several nunatak areas known, where the last glaciers did not develop or where their work was so restricted as to leave essentially undisturbed some regions of mountains, high plateaus and precipitous headlands and, in the famous "driftless area" of Wisconsin, Illinois, Iowa and Minnesota, even of prairie. In the area we are specially considering the most notable of these nunataks[1] or regions unglaciated or only slightly denuded by the last continental ice-sheet are the Torngat Mountains, just south of the eastern entrance to Hudson Strait, large areas of Newfoundland, especially centering on the Long Range near the West Coast, the eastern half of the Gaspé Peninsula of Quebec, and some other smaller and isolated spots about the Gulf of St. Lawrence.

Temperate eastern North America has, then, an extensive area (the southern Appalachian Upland) in which land-plants have had an opportunity to spread since the advent of Angiosperms; others (limited portions of the inner Coastal Plain and much of the central plain of the United States) where living floras could have taken possession only after the withdrawal of the Cretaceous seas; others (much of the

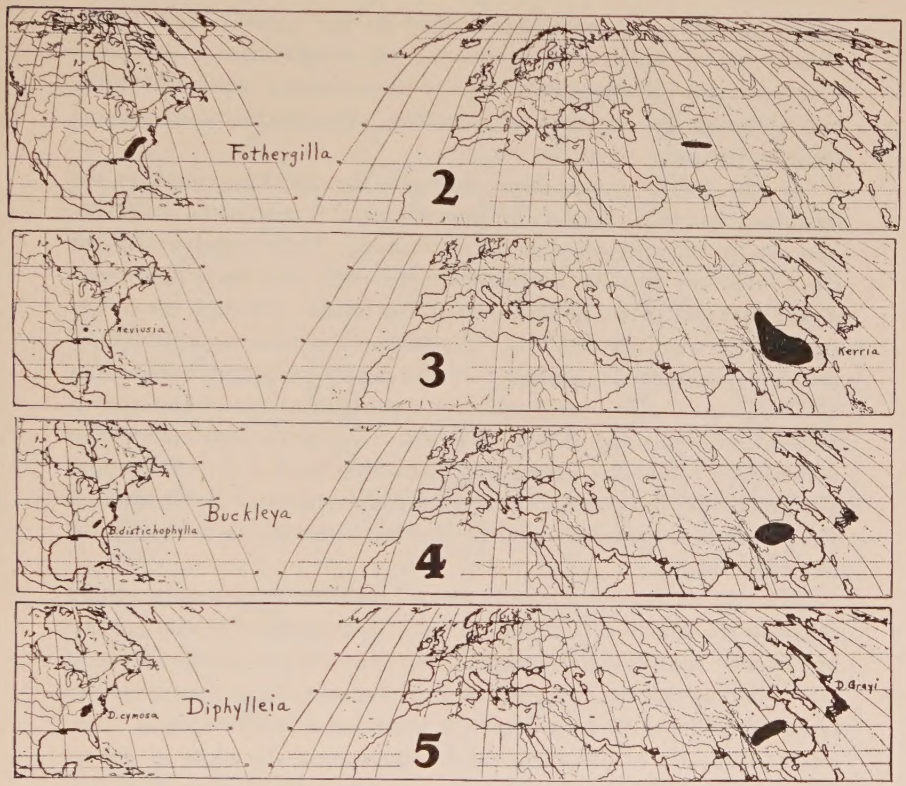
[1] For enumeration and discussion of these areas see Fernald, *Persistence of Plants in Unglaciated Areas of Boreal America*, Mem. Amer. Acad. xv. No. III. (Mem. Gray Herb. ii.) 295–317 (1925).

Atlantic and Gulf Coastal Plains) unavailable to land-plants until the tipping off of the Eocene and the Miocene waters; others (the nunatak areas) which apparently retained their present distinctive floras through at least the last glaciation; still another, the largest of all, the vast region of Canada and the Northern States which has become available for wholesale occupation by plants only since the decay of the Wisconsin ice, within the last few thousand years; almost as young or in some regions even younger, scattered areas at the outer margin of the Coastal Plain, of very recent or Quatenary origin; and, youngest of all, the million or more square miles cleared and fundamentally altered by the white man during the last three centuries.

These strongly contrasted periods of availability to plant-populations of different eastern American areas are, of course, closely paralleled in other regions: for instance, in Europe, with the western third of the Iberian tableland uninvaded by the Cretaceous and the Tertiary seas which drowned much of the continent; others, like much of the Mediterranean basin, largely unavailable until the withdrawal of the Tertiary seas; and still others, such as southern Scandinavia, only a few thousand years removed from submergence under the Great Baltic Glacier. The distinctive floras which characterize the different physiographic areas of temperate eastern North America are very definite, and it is my purpose, in so far as time will allow, to direct attention to the different degrees of specific segregation shown, especially by the amphigean or the world-wide genera in these different floras.

In the ancient Appalachian Upland of the United States the outstanding phytogeographic feature is, of course, the great mesophytic forest of Mesozoic or early Cenozoic genera, many of them formerly found likewise in Europe, western America and the Arctic but now restricted to one or more areas of eastern North America, eastern, central or southwestern Asia[1] or the geologically ancient peninsulas of

[1] The identity or close similarity of angiospermous genera of eastern Asia and eastern North America was recognized as early as 1750 by Halen, a student of Linnaeus, who, in his thesis, *Plantae Camschatcenses Rariores*, pointed out (in § V) several such cases—see L. Amoen. Acad. ii. 336 (1751). This relationship has subsequently been frequently emphasized and many typical examples are well known. Consequently, only a few illustrations, perhaps less generally familiar, are here enumerated. Other cases are discussed in the following papers by myself: *The Geographic Affinities of the Vascular Floras of New England, the Maritime Provinces and Newfoundland*, Am. Journ. Bot. v. 228 (1918); *Isolation and Endemism in Northeastern American and their Relation to the Age-and-Area Hypothesis*, Am. Journ. Bot. xi. 570 (1924); *The Antiquity and Dispersal of Vascular Plants*, Quart. Rev. Biol. i. 222, 227, 229 (1926); *Some Relationships of the Floras of the Northern Hemisphere*, Proc. Intern. Congr. Pl. Sci. ii. 1489 (1929).



Map 2, Geographic Range of FOTHERGILLA; 3, of KERRIA, and its American Representative, NEVIUSIA; 4, of BUCKLEYA; 5, of DIPHYLLEIA.

southeastern Europe: *Fothergilla* (MAP 2)[1] with a few excessively rare species in the southern Appalachians and one on the wooded slopes of Kashmir and adjacent Afghanistan; *Hamamelis*, with wide-ranging eastern American species and localized Asiatic representatives; *Magnolia*, highly developed in both southeastern North America and southeastern Asia; *Neviusia* (MAP 3), like an apetalous representative of the local Chinese *Kerria*[2] and known only from a very restricted station in the foothills of Alabama; *Pachystima, Stewartia, Symplocarpus, Panax, Shortia, Phryma, Triosteum* and scores and scores of others. It was this vast assemblage in the southern Appalachian

[1] The world-maps used to show ranges of plants in this paper are made on Goode's Homolographic Projection, published and copyrighted by the University of Chicago.

[2] *Kerria japonica* DC., in spite of its specific name, is endemic in China.

region as well as the remarkable relics on the Coastal Plain of the United States which stimulated Guppy, congratulating American students upon the superabundance of these ancient types still living and picturing the emotions of a student appreciative of his opportunity, to write:

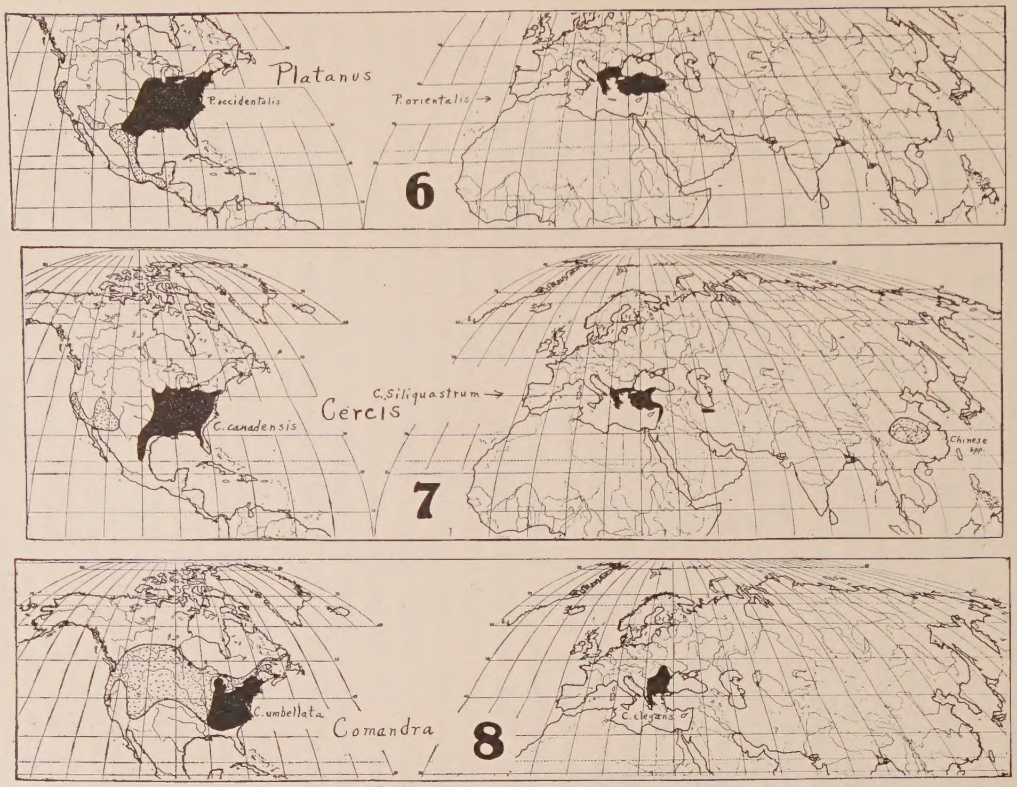
"In the woods around him were growing the Liquidambar, the Sassafras, and other shrubs and trees that had flourished in the Mesozoic ages in the spot where he was standing. Their remains crowded the Cretaceous deposits exhibited in the cliffs near by. Specimens of the past and of the present were in his hands. Though the difference in kind was very slight . . . the difference in time, measured in human lives, amounted to eternity. It is a story of perpetuity rather than of change . . . He begins with the cosmopolitanism of such types in the Cretaceous age and he ends with their more restricted distribution and somewhat greater specialization now. . . . Those old genera become the genera of today; and the genera of today, though the genera of a thousand ages, are 'but as yesterday' in the history of flowering plants."[1]

Not only, as Guppy so vividly stated, are these Appalachian genera of today the genera of a thousand ages; their species are also ancient and usually sharply differentiated. No one with good material would fail to distinguish the two or three local Japanese and Chinese species of *Buckleya*[2] from the famously rare American *B. distichophylla* Torr. (MAP 4), the latter American shrub parasitic on the roots of *Tsuga*, the American *Menispermum canadense* L. from the Asiatic *M. dauricum* DC., the extremely local American *Cladrastis lutea* (Michx.) K. Koch from the Japanese *C. platycarpa* Mak. and the other Asiatic species; nor such herbs as the highly localized Appalachian *Diphylleia cymosa* Michx. (MAP 5) from the less localized Asiatic *D. Grayi* F. Schmidt, or the American *Podophyllum peltatum* L. from the Asiatic *P. emodi* Wall. Such illustrations of this eastern Asiatic-eastern American generic similarity but specific differentiation could be increased by hundreds but these must now suffice.

Turning to genera, subgenera or sections shared by Appalachian America and eastern or southeastern continental Europe, we again get sharp specific differentiations: the Old World *Platanus orientalis*

[1] Guppy, *Fossil Botany in the Western World: an Appreciation*, Am. Journ. Sci. ser. 4, xlix. 372 (1920).

[2] For memoranda on the Asiatic ranges of *Buckleya* and some other genera I am indebted to the kindness of Dr. Handel-Mazzetti.



Map 6, Geographic Range of PLATANUS; 7, of CERCIS; 8, of COMANDRA.

L. (map 6) and the American *P. occidentalis* L. (with some related trees farther west); the Appalachian *Anemone lancifolia* Pursh, which has generally been confused with the European *A. trifolia* L. but which differs[1] in constant details of the flowers; the Eurasian *Cercis Siliquastrum* L. (map 7) and the American *C. canadensis* L., with other species in western North America and in central China; the common American genus *Comandra* (map 8) with a single Eurasian representative, the comparatively localized *C. elegans* (Rochel) Reichenb.; and so on through dozens of groups, the southeastern European and the eastern American species usually having western North American representatives as well. In the cases just cited the Appalachian and the Old World species are sharply distinguished, but there are a few (perhaps a dozen) cases of Angiosperms (and still more in the Pteridophytes) where the differentiation of species is not so complete, the eastern American and the Asiatic plants being considered by some systematists as recognizable species, by others as merely geographic varieties: such cases as *Tovara virginiana* (L.) Raf., *Polygonum sagittatum* L., *Liriodendron Tulipifera* L.,[2] *Phryma Leptostachya* L. and *Aruncus sylvester* Kosteletz.; while in a few cases, such as *Symplocarpus foetidus* (L.) Nutt. and *Monotropa uniflora* L., search has failed to reveal even significant varietal differences. Admitting these very few exceptions (which will become significant when we have examined the historical relation of the mesophytic Alleghenian flora to the prevailingly xerophytic and hydrophytic Coastal Plain groups), however, when the hundreds of species of Appalachian angiospermous genera are compared with their Old World representatives the general conclusion is

[1] See Fernald, Rhodora, xxx. 184 (1928).

[2] There is a very general impression that *Liriodendron* is one of the most ancient of Dicotyledons and that its antiquity is demonstrated by its having occurred in Greenland during the Cretaceous. The error involved has been well summarized by Seward: "Among the numerous species of Dicotyledons are some which it has been customary to refer to the genus *Liriodendron*, now represented by the Tulip-tree of North America and China. A recent examination of specimens [from Greenland] of these simple, emarginate 'leaves' has convinced me that they are the leaflets of a compound leaf, a conclusion which had previously been reached by some other palaeobotanists who have examined specimens from North American and European Cretaceous rocks. In a recently published book on 'Tree Ancestors,' the American palaeobotanist, Mr. E. W. Berry, speaks of the occurrence of *Liriodendron* in Greenland, but I venture to think that there is no satisfactory evidence in support of this statement. Though it is not possible from the available material to refer the leaflets to any one recent genus with complete confidence, the probability is that they belong to compound leaves of a plant closely allied to some existing species of *Dalbergia* or possibly *Pterocarpus*, genera with a wide geographical distribution in the tropics and both occupying a similar position in the Leguminosae."—Seward, *Arctic Vegetation Past and Present*, Journ. Royal Hort. Soc. l. pt. 1: 15 (1925).

apparent: that in nearly all groups the species of the Western Hemisphere are completely segregated from those of the Eastern; that we here have stable or essentially stable specific entities.

Descending to the broad outer Coastal Plain of Atlantic North America, the region of silicious and acid peaty soils of Tertiary or later origin, we come to a change in the flora so striking as immediately to challenge attention; for, whereas the distinctive non-endemic genera of the southern Appalachian region are those shared with temperate eastern and central Asia or with southern or eastern Europe, the Old World elements in the indigenous Coastal Plain flora of Atlantic North America are prevailingly the groups with wide tropical and subtropical range, the families, tribes, genera and sections shared by the Americas with tropical and subtropical Africa, tropical and subtropical Asia, and Australia but for the most part unknown in temperate Europe and largely unrepresented in temperate Asia. For instance, if I may be permitted to leave for a moment the Angiosperms and to draw an illustration from the Pteridophytes, the ancient genus *Schizaea* (MAP 9), with 20–25 species confined to the Southern Hemisphere and the Tropics, in the Old World unknown north of Madagascar, the Seychelles, India and the Philippines; in the New World wanting north of tropical Mexico and subtropical Florida, but with the single famous exception, *Schizaea pusilla* Pursh. This solitary northern species was long supposed to be restricted to a limited area of the northern Coastal Plain, in New Jersey, but we now know that the regions of its wide-spread abundance are the peats of more northern Nova Scotia and still more northern Newfoundland; *S. pusilla* on the latter island being a typical species both of the highest unglaciated tablelands and of the lower regions recently covered by Wisconsin ice. Very similar tropical or austral relationships are shown by the majority of non-endemic genera and tribes of Angiosperms (and especially of Monocotyledons) on the Atlantic Coastal Plain: the *Haemadoraceae* (MAP 10) restricted to Australia, South Africa, tropical America and the Atlantic Coastal Plain north to Massachusetts; the tribe *Conostylideae* (MAP 11) of the *Amaryllidaceae* with 50 species in southwestern Australia, 1 in South Africa and 2 in eastern North America, the American species both excessively local but one of them extending north to Nova Scotia; the *Xyridaceae* (MAP 12) confined to the Southern Hemisphere and the Tropics except for an extension northward along the eastern margin of North

Map 9, Geographic Range of SCHIZAEA, S. PUSILLA in ellipse; 10, of the HAEMADORACEAE.

Map 11, Geographic Range of the Amaryllidaceae, Tribe Conostylideae; 12, of the Xyridaceae.

America quite to latitude 50° in Newfoundland, with a slight isolation inland in the north about the Great Lakes and an area of disrupted colonies (of *X. torta* Sm.) on the 4000-foot silicious tablelands of the southern Appalachians; and so on with prevailingly tropical or austral groups like *Lophotocarpus, Eriocaulon, Hypoxis, Drosera* (map 28), *Galactia, Lilaeopsis*, the *Pontederiaceae, Burmanniaceae, Podostemaceae* and hundreds of other groups.

Although the eastern American representatives of the tropical and austral groups are there now concentrated on the soils of Tertiary, Quaternary or even Pleistocene origin, they are by no means restricted to the comparatively youthful areas. Here and there along the ancient tableland-crests of the Appalachian system, wherever the primitive, open xerophytic or hydrophytic conditions prevail and where the denuding action of the Pleistocene ice was not too severe, we are learning to expect rare and highly localized members of the so-called Coastal Plain flora, like *Xyris torta* (map 31) just referred to. Through Mesozoic time the Appalachian Mountains of the present day did not exist as mountains but, as Berkey succinctly puts it, "The continent stood much lower than now. Portions that are now mountain tops and the crests of ridges were then constituent parts of the rock floor of the peneplain not much above sea level. . . . Such conditions prevailed over a very large region—certainly all of the eastern portion of the United States."[1] The following, from among the very numerous corroborative statements, are representative of the consensus of geological opinion. "Jurassic time throughout the greater part of North America was one of erosion. . . . This erosion cycle brought about the final transformation from the old topographic expression of high Appalachian . . . mountains to a nearly base-leveled land."[2] "Once more there was prolonged quiet. The fault-block mountains were persistently attacked by the erosive agents and were reduced [in early Cretaceous], like their Appalachian predecessors, to an almost plane surface, close to sea-level."[3] "It is known as the 'Cretaceous Peneplain,' because of its best development during the Cretaceous period. This vast plain extended over the areas of the Appalachian Mountains, Piedmont Plateau, all of New York state, the Berkshire Hills, and the Green and [the] White Mountains. . . . . The Cretaceous period was closed in eastern North America

[1] Berkey, N. Y. State Mus. Bull. no. 146: 67 (1911).
[2] Schuchert, Historical Geol. 846 (1915).
[3] Daly, Our Mobile Earth, 297 (1926).

by a disturbance which produced an upwarp of this vast Cretaceous peneplain with maximum uplift of from 2000 to 3000 feet . . . to produce a broad dome sloping eastward and westward, and northward to the Gulf of St. Lawrence and southward to the Gulf of Mexico."[1]

And studies by the geologists farther north clearly indicate that the peneplained or baseleveled condition of the ancient mountain-axes extended at least to Newfoundland and apparently to northern Labrador, if not beyond. For example, Alcock, reporting on the Shickshock Mountains of Gaspé, famous, like the tablelands of western Newfoundland, for having stood undisturbed above the local ice-sheets of the Pleistocene,[2] says: "Gaspé peninsula . . . is a region of Appalachian structure, . . . The interior of the peninsula is a plateau dissected by deep valleys . . . The most striking feature is, probably, the mature character of the upland topography . . . the skyline is comparatively even in all directions. . . . Gaspé peninsula, therefore, is a region which must have been base-leveled and, later, uplifted and dissected. . . . A youthful topography, represented by these steep-walled valleys, is superimposed upon the old age topography of the upland surface."[3] Similarly, Twenhofel, whose intimate knowledge of the physiography of the region is unequaled, says: "To one approaching Newfoundland from Sidney [Cape Breton] . . . , the most impressive feature is the high flat-topped upland, here rising almost vertically from the sea. . . . If Newfoundland be observed from the Labrador side, one feature will attract and maintain the attention: the flat-topped upland, standing boldly and prominently in view. . . . The sky line of the Long Range is strikingly horizontal and the appearance of an equal height in all its parts is not a fiction resulting from a distant view, for it remains the same near as well as far. . . . The accordance of the summit levels of the highlands, . . . the presence of well preserved flat-topped mountains at many localities with the projected plane of their summits

[1] Miller, Historical Geol. ed. 3: 278, 279 (1928).

[2] "There is no evidence that glaciers worked on the highest parts of the Shickshock mountains"—Coleman, *Physiography and Glacial Geology of Gaspé Peninsula, Quebec*, Can. Dept. Mines, Geol. Surv. Bull. 34 (1922); "The Shickshock Mountains, though occupied by local glaciers during the Pleistocene, escaped the erosion of the continental ice sheets."—Alcock, *Across Gaspé*, Geogr. Rev. xiv. 208 (1924); "the southern part of the Long Range . . . seems to have remained as an area free from ice on which pre-glacial plants could survive."—Coleman, *The Pleistocene of Newfoundland*, Journ. Geol. xxxiv. 220 (1926).

[3] Alcock, *Geology of Lemieux Township, Gaspé County, Quebec*, Geol. Surv. Can. Summ. Rep. 1921, Pt. D, 76, 77 (1922).

truncating all kinds of structure and rock, . . : these are considered evidence of the present dissection, but one time perfection of a peneplain, a plain of erosion of remarkable perfection extending over the whole of Newfoundland. . . . . On this ancient plain the rivers were free to wander where they would, ... They probably crossed the site of the present mountain ranges and, when the land arose, each stream struggled to maintain its position. . . . In the eastern United States throughout the Appalachians, the existence of an extensive peneplain, completed before the end of Cretaceous time, is now universally admitted and with this base level that of Newfoundland is tentatively correlated, and the period of development and close of the cycle assumed to be the same."[1] Beginning with the close of the Cretaceous and continuing, with minor interruptions, through Tertiary time this floor of ancient Appalachian rock, only slightly above sea-level, was gradually uplifted and deeply weathered and sculptured to produce the Appalachian Upland of today; and as the upwarping of the older land progressed the marginal region, which had been overlapped by the shallow Tertiary seas, was also elevated, tipping off the Tertiary waters and extending the emerging continent a full 100 miles (160 kilometers) eastward to the margin of the now submerged continental shelf. The American geologist, Miller, thus puts the matter: "The uplift of the great Cretaceous peneplain was an event of prime importance for the eastern United States, because it literally furnishes us with the beginning of the history of most of the existing relief features of the Appalachian district as well as New York and much of New England. Hence we assert, with emphasis, that all the principal topographic features of this region as we see them today date from the uplift of the Cretaceous peneplain, because they have been produced by the dissection of that upraised surface. This dissection was largely the work of erosion. . . . . All the valleys, great and small, such as the Champlain, Connecticut, Mohawk, Hudson, the Great Lakes valleys, and the valleys of the Appalachians, have been produced since the uplift of the peneplain."[2]

In view of this well attested physiographic and ecological change of the Appalachian Upland, from a baseleveled or coastal-plain status, with sluggish drainage and innumerable shallow pools and boggy de-

[1] Twenhofel, *Physiography of Newfoundland*, Am. Journ. Sci. ser. 4, xxxiii. 7, 18, and 19 (1912).

[2] Miller, Hist. Geol. ed. 3: 326–329 (1928).

pressions through much of the Cretaceous, to its present elevated and deeply dissected condition, it is certainly significant that in favorable habitats at different points on the now uplifted ancient peneplain we find relic-colonies of such tropical or austral genera as *Schizaea*, *Lygodium*, *Stenophyllus*, *Eriocaulon*, *Xyris*, *Lobelia* and that peculiar terrestrial group of *Utricularia*, sometimes treated as a genus, *Stomoisia*, with 50 species in tropical Asia, Africa, Australia, eastern South America and eastern North America; and mingled with the typical lowland plants of tropical or austral affinity on the high Appalachian crests and tablelands we sometimes find similar relic-colonies of characteristic endemic American genera of the Atlantic Coastal Plain: *Orontium*, *Xerophyllum*, *Helonias*, *Calopogon*, *Cleistes*, *Sarracenia*, *Hudsonia*, *Rhexia*, *Leiophyllum*, *Bartonia* and numerous others. *Schizaea pusilla* of the Pine Barrens of New Jersey and of the peaty barrens of Nova Scotia and Newfoundland occurs, likewise, on the highest unglaciated tablelands (the uplifted Cretaceous peneplain so much enphasized above) of Newfoundland. My first experience with it was on the diorite tableland of the Blomidon Range, my published note reading: "Among the tufts of *Scirpus caespitosus* . . . was the famous little fern of the New Jersey Pine Barrens, *Schizaea pusilla*. . . . . Here at 2000 feet altitude it abounded over many acres, nestling in the bases of the *Scirpus* tussocks."[1] Fifteen years later the great student of Pleistocene geology, Coleman, visiting Blomidon, wrote: "From this [1,560 feet] to the highest point reached (1,700 feet) . . . there was no evidence of glaciation."[2] *Lygodium palmatum* (Bernh.) Sw., the only living member of this tropical genus now found on the Appalachian tablelands, has upland stations scattered from western New England to Tennessee; *Eriocaulon septangulare* With., *Xyris montana* Ries, *Lobelia Dortmanna* L. and *Utricularia* (*Stomoisia*) *cornuta* Michx. abound in pools on the tablelands of Newfoundland, there often associated with *Schizaea pusilla;* the *Eriocaulon*, *Xyris*, *Utricularia* and *Lobelia* also occurring, along with the Coastal Plain *Lygodium palmatum*, *Orontium aquaticum* L., *Amianthium muscaetoxicum* (Walt.) Gray, *Aletris farinosa* L. and *Rhexia virginica* L. on the tablelands of Pennsylvania.[3] *Xerophyllum asphodeloides* (L.) Nutt. and *Zigadenus leimanthoides* Gray, ordinarily Coastal Plain plants, have long been known from the high tablelands of North

[1] Fernald, Rhodora, xiii. 133 (1911).
[2] Coleman, Journ. Geol. xxxiv. 210 (1926).
[3] Porter, *Flora of the Pocono Plateau*, Rhodora, i. 183–185 (1899).

Carolina; *Leiophyllum prostratum* Loudon and *L. Hugeri* (Small) K. Sch. are the Appalachian crest representatives of the Coastal Plain *L. buxifolium* (Berg.) Ell. *Helonias bullata* L., for nearly two centuries supposed to be endemic on the Coastal plain, was found[1] in 1909 on the mountains of western North Carolina; and *Cleistes divaricata* (L.) Ames (*Pogonia divaricata* R. Br.), also considered a typical species of the Coastal Plain, is well known from high tablelands of the southern Appalachians.[2] In fact, this relationship of the Coastal Plain and the Appalachian tablelands has long been known. Thus, in 1879, Redfield, describing the Carolina mountain trip with Canby, Gray, Hyams and Sargent, wrote: "on the 12th was made the ascent of Table Rock, a most remarkable summit, belonging to the Blue Ridge system, presenting in one direction the tabular profile which gives it its name, and from another a sharp conical outline not unlike that of the Matterhorn. The botanists returned from it laden with plants, and it was curious to see among them so many of the species which are associated with the sandy barrens and swamps of southern New Jersey."[3]

In some cases plants of Australian, Malayan and African affinity are now found in America almost wholly in the North, in the region which was largely under the Pleistocene ice. This most unlooked-for disruption of range is well illustrated by *Potamogeton*, sub § *Javanici* (map 13), the group of dimorphic plants which Hagström considered the most primitive of pondweeds with floating leaves The members of this primitive subsection occur locally in Australia, more generally from Java to Japan and Burma, on Madagascar and across southern and central Africa; but outside these tropical and subtropical areas of the Old World the *Javanici* are known only as two extremely rare species, so rare that each new station is heralded as a notable range-extension, *Potamogeton Vaseyi* Robbins and *P. lateralis* Morong, confined to a limited region of the northeastern United States and adjacent Canada. A very similar disruption is displayed by *Myriophyllum*, § *Tessaronia*, the plants of *Eumyriophyllum* with four, instead of eight, stamens, plants of tropical and subtropical India, Madagascar and eastern North America, but with a slight representation also in Pacific North America.

[1] House, Muhlenbergia, vi. 73 (1910).

[2] Gattinger, Tenn. Fl. 84 (1887); Small & Heller, Mem. Torr. Bot. Cl. iii. no. 1: 10 (1892); Kearney, Plant World, i. 35 (1897); Wherry, Journ. Wash. Acad. Sci. xviii. 213 (1928).

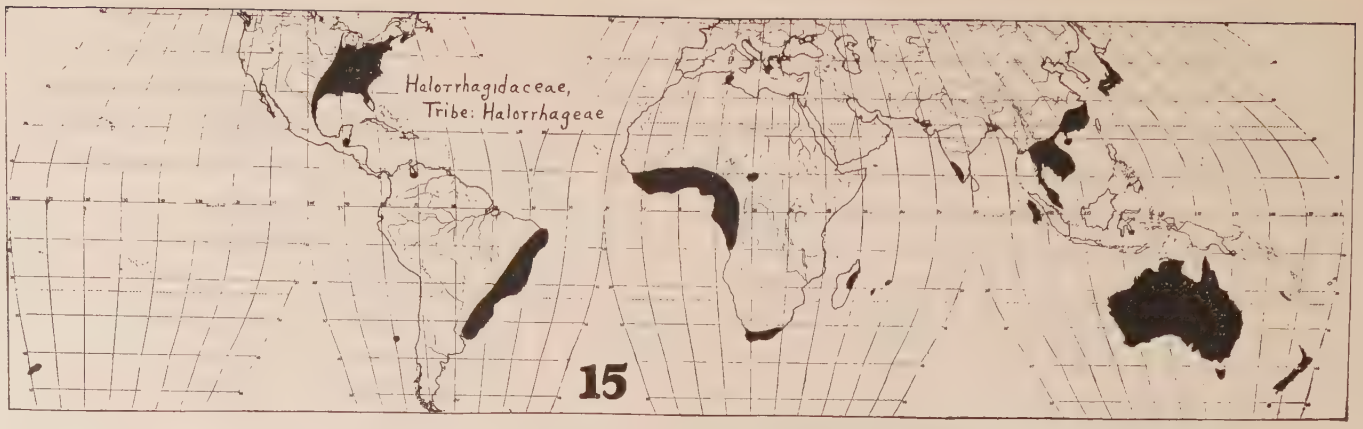
[3] Redfield, Bull. Torr. Bot. Cl. vi. 335 (1879).

Map 13, Geographic Range of Potamogeton, sub § Javanici; 14, of Diospyros.

Whether the wide-ranging herbaceous angiospermous groups of the Atlantic region of North America were Mesozoic or early Cenozoic genera of the whole Northern Hemisphere, which have subsequently restricted their ranges principally to the Tropics, we cannot now absolutely demonstrate. As herbs they have left few if any fossils; but Carboniferous, Jurassic and Cretaceous members of the *Schizaeaceae* occurred in Europe and northern Asia, even in arctic Spitzbergen;[1] and the ligneous and consequently easily fossilized genus *Diospyros* (map 14), which today has an essentially tropical distribution quite comparable with the present ranges of *Schizaea*, *Lygodium*, *Potamogeton*, sub § *Javanici*, *Lophotocarpus*, *Xyris*, *Eriocaulon*, the *Burmanniaceae* (map 18), the *Droseraceae* (map 28), the *Halorrhagidaceae*, tribe *Halorrhageae* (map 15) and hundreds of other groups (except that, unlike them, *Diospyros* is considered indigenous also from northern India to the Caucasus and the Black Sea), in mid-Cretaceous covered practically the whole Northern Hemisphere, quite to the Arctic. Berry's vivid account is to the point: "In that grand display of dicotyledonous genera which during the mid-Cretaceous replaced the old Mesozoic flora of ferns, cycads, and conifers and which appeared with such apparent suddenness at a number of points in the Northern Hemisphere, we find unmistakable evidence of the abundance and wide distribution of species of Diospyros. No less than 17 different forms have been described from the rocks of this age, and the localities where they have been found are scattered from Australia to Bohemia, Greenland, and Vancouver Island . . . . they seem to have been especially at home along the Cretaceous coast of the Atlantic and along the border of the Mediterranean Sea which extended northwestward from the Gulf of Mexico over much of our present Great Plains area."[2] In other words, their greatest display of Cretaceous fossils is in the margin of the area covered by the Cretaceous seas, which then bordered the baseleveled land which in the Tertiary became uplifted and dissected to form the present Appalachian Upland with its characteristic climax mesophytic forest. Very similarly, ligneous *Nyssa* (map 16), today with a disrupted range somewhat similar to that of *Myriophyllum*, § *Tessaronia*, formerly had a broad range across Eurasia and North America, reaching Spitzbergen and

[1] See Potonié in Engl. & Prantl. Naturl. Pflanzenfam. i.[4] 372 (1900); also Seward, *A Study in Contrasts: The Present and Past Distribution of certain Ferns*, Journ. Linn. Soc. xlvi. 233, 234 (1922).

[2] Berry, Tree Ancestors, 257 (1923).



Map 15, Geographic Range of the HALORRHAGIDACEAE, Tribe HALORRHAGEAE; 16, of NYSSA.

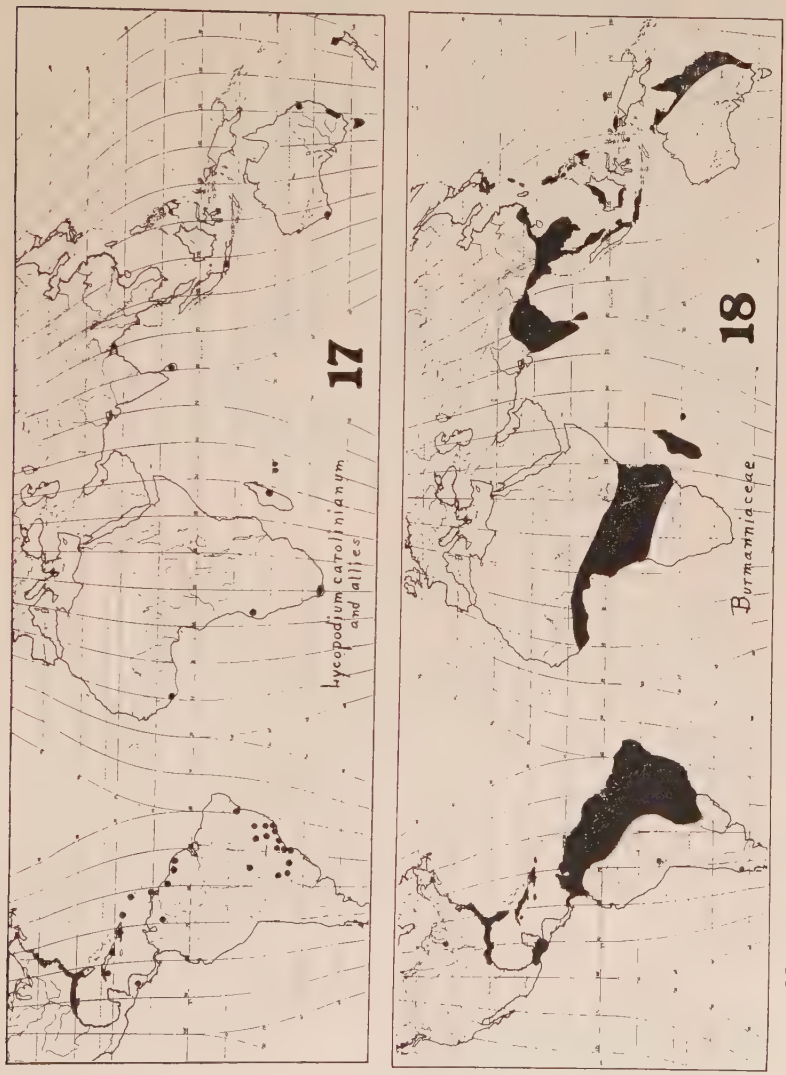
Greenland. Again drawing upon Berry's *Tree Ancestors:* "A large number of fossil forms of gums have been described . . . found in Upper Cretaceous deposits in Wyoming, Nebraska, Kansas, and Alabama. During the early Tertiary gums are extraordinarily abundant. . . . It is worthy of comment that all of the Upper Cretaceous and Eocene gums are North American or Arctic, . . . In the far north they occurred at that time in Alaska, Greenland and Spitzbergen."[1] This present restriction primarily to the Tropics of groups formerly wide-spread in the Arctic has been summarized by our President in a single sentence: "A study of ancient floras reveals the capacity of plants as travelers; many flowering plants, conifers, and ferns that are now confined, or almost confined, to the tropics of the southern hemisphere were in the Cretaceous and Tertiary periods represented by species widely spread over the northern hemisphere, passing far within the Arctic Circle."[2] And all of us will call to mind groups, prevailingly tropical today, which are also characteristic of temperate Atlantic North America and which have a few northern representatives in Europe as well: *Eriocaulon*, *Echinodorus*, *Fuirena*, *Fimbristylis*, *Mariscus* (*Cladium*), *Smilax*, the *Dioscoreaceae*, *Hibiscus* and *Ammania*.

A few species in eastern North America have today ranges quite comparable, except for minor details, with that of *Schizaea pusilla*, admittedly a relic from the boreal Cretaceous or earlier dispersal of its progenitors. This parallelism of range (on some of the Appalachian plateaus, uplifted from their sea-level position of the Cretaceous, and on the Atlantic Coastal Plain or its margin, with few if any intermediate stations) is well shown by one of the most distinct and rarest of pondweeds, *Potamogeton confervoides* Reichenb. (PLATE 204; also MAP 33). This remarkable species has the free ligules and continuous spike of the comparatively advanced subgenus *Eupotamogeton;* it constitutes Hagström's subsection *Monticoli* of *Eupotamogeton*, but, as he has stated, it exhibits such primitive anatomical characters as to form a "transition to the [primitive] *Coleogeton* species";[3] and in its delicate foliage, its branching, its creeping rhizome with subterranean tubers, and its long, terminal peduncle it so strongly simulates *P. pectinatus* L. (PLATE 204), *P. filiformis* Pers. and other species of the most primitive subgenus *Coleogeton* that only by the closest examin-

[1] Berry, l. c. 244.

[2] Seward, Journ. Royal Hort. Soc. l. pt. 1: 17 (1925).

[3] Hagström, *Critical Researches on the Potamogetons*, Kungl. Svenska Vetenskapsakad. Handl. lv. No. 5: 86 (1916).



Map 17, Geographic Range of Lycopodium carolinianum and Allies; 18, of the Burmanniaceae.

ation can it be distinguished from them. It certainly is not a mere accident that today the obvious relic-species, *Schizaea pusilla*, on the uplifted Cretaceous peneplain of Newfoundland (and apparently also of Cape Breton) should there border the shallow pools in which the rare and demonstrably primitive *Potamogeton confervoides* is found; nor that these two, along with the equally rare and ancient *Lycopodium carolinianum* L., should be close neighbors in that haven of relic-species, the Pine Barrens of New Jersey, for, surely, the amazingly disrupted austral occurrence (MAP 17)[1] of restricted colonies of *L. carolinianum* and its immediate allies[2] is good evidence, if evidence were needed, that that species (in the broad sense) is of great antiquity. It is also not a mere accident that except for rare stations in the silicious Coastal area, *P. confervoides* should be known in Pennsylvania, New York and New England only in pools on or among the highest mountains ("Alleghany Mountains," sent by Schweinitz to Reichenbach; Pocono Plateau, Pennsylvania, where associated with the relic colonies of Coastal Plain types enumerated on p. 39; Adirondack Mts., New York; Taconic and Green Mts., Massachusetts and Vermont; White Mts., New Hampshire; Mt. Katahdin, Maine).

The present-day ranges of the tropical groups which are represented in temperate eastern North America closely coincide with the existing continental and insular remnants of hypothetical Gondwana, the great equatorial land which, in the Permian, is supposed by some to have stretched from Australia and peninsular India to Africa and South America. But those who have reconstructed Gondwana Land (MAP 19)[3] tell us that, in Lower Cretaceous time Gondwana had become much disrupted and that by mid-Cretaceous (MAP 20) it had broken into remote Australia, Lemuria, Ethiopia, and Amazonia. Furthermore, during the supposed existence of Gondwana that equatorial land has been pictured as having had no direct connection with the Atlantic United States, and subsequently (MAPS 22–27)[4] the gap between the southeastern United States and Brazil is said to have been

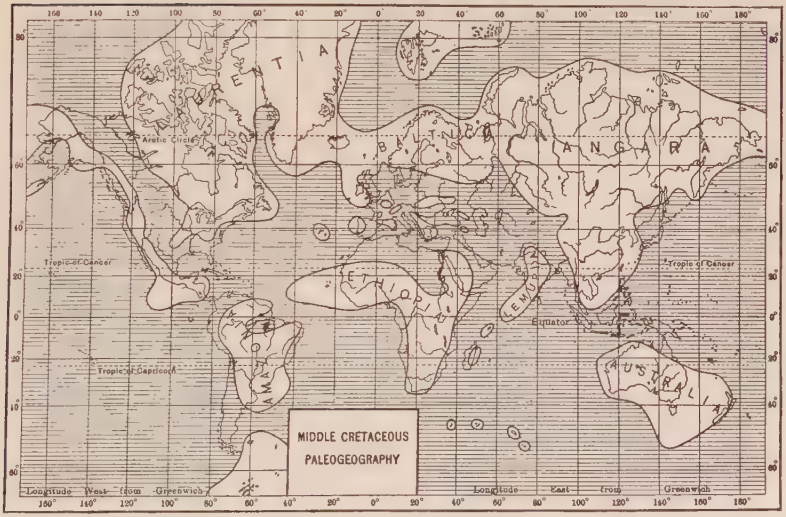
[1] Doubtless a few tropical and austral stations have been overlooked, since most "Floras" omit the Pteridophyta.

[2] Including *L. drepanoides* Blume, *L. Drummondii* Spring, *L. goyozense* and *L. meridionale* Underw. & Lloyd, *L. paradoxum* Spring, *L. sarcocaulon* Welw. and *L. tuberosum* A. Br.

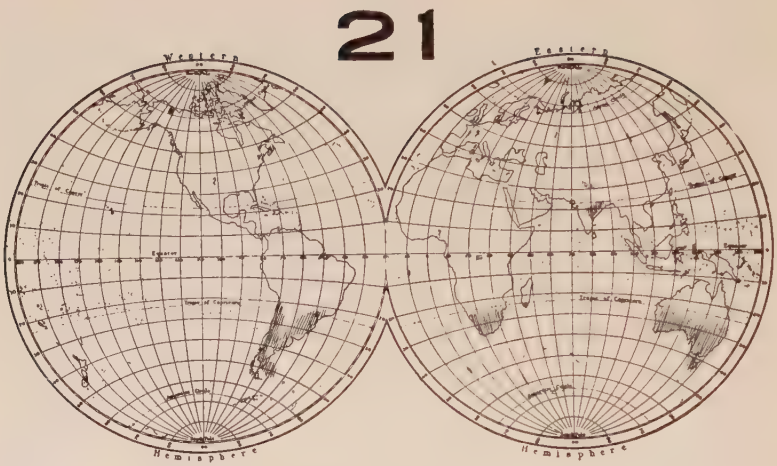
[3] Map 19 is copied, with permission, from Schuchert, Hist. Geol. fig. 434 (New York, John Wiley & Sons, Inc.); map 20 from Schuchert's fig. 488.

[4] Maps 22–27 are from Schuchert, *Geological History of the Antillean Region*, Bull. Geol Soc. Am. xl. 337–360 (1929).

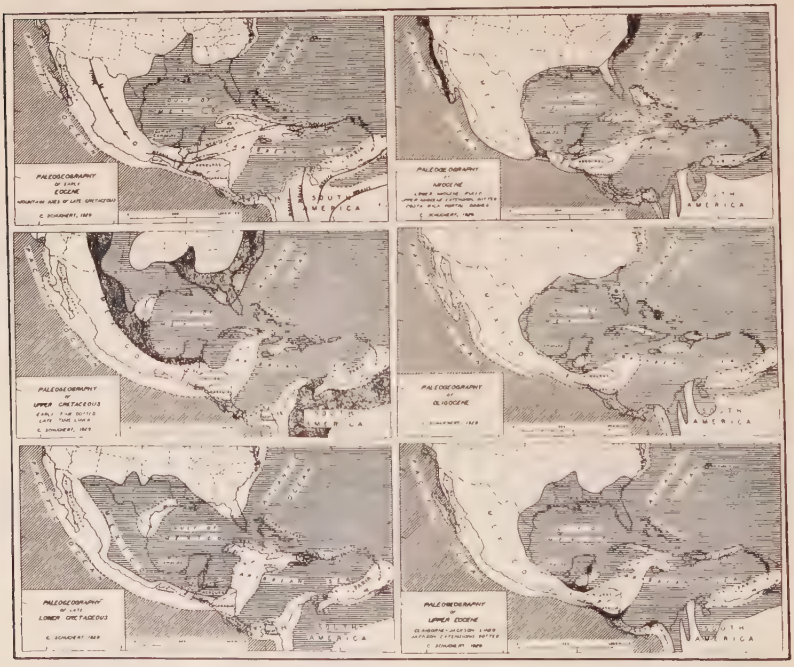
Map 19, the World in Permian time (after *Schuchert*).



Map 20, the World in Mid-Cretaceous time (after *Schuchert*).



Map 21, the PERMIAN GLACIATION (after *Coleman*)



Map 22 (lower left), Geographic Connections of the Antilles in the LOWER CRETACEOUS; 23 (middle left), in the UPPER CRETACEOUS; 24 (upper left), in the early EOCENE; 25 (lower right), in the UPPER EOCENE; 26 (middle right), in the OLIGOCENE; 27 (upper right), in the MIOCENE (all after *Schuchert*).

continuously maintained and often broadened. Consequently, Gondwana, as usually defined and whether a hypothetical or a demonstrated Permian land, need not necessarily concern our immediate problem. If, however, with Alphonse De Candolle and many other thoughtful students, we conceive the angiospermous groups of today as having lived in Jurassic time[1] or if, with Velenovský, Mrs. Arber[2] and numerous others, we push the ancestral Angiosperms (the Protangiosperms of Engler[3]) back beyond the Cretaceous, and also greatly extend the area of Gondwana in the Western Hemisphere to reach the southeastern United States, then that hypothetical equatorial land will immediately come into the picture. In this connection it is worth noting that my associate, Dr. Hugh M. Raup, calls attention to the very striking fact, that hundreds of tropical and austral groups of today have restricted ranges almost coincident with the known areas of Permian or Permo-Carboniferous glaciation (see MAPS 21 and 19; also MAPS 9–18). If, indeed, Angiosperms existed at that time and if youthful and aggressive groups then spread into newly available territory as do virile and dominating groups today, it would seem only natural that, with the decay of the Permian glaciers, the most aggressive plants of the adjacent territory should quickly have taken possession and that their descendents should still linger about their ancestral centers. By some the herbaceous habit is associated with cold climates, and many herbs (as well as shrubs and trees) undoubtedly originated during the Pleistocene, while many others seem to be even more youthful; but, surely, many of the herbaceous species of today are as ancient as their living ligneous associates. And it is certainly significant that the greatest glaciation in the history of the world was the Permo-Carboniferous (MAP 21).[4] If it be true that the development of herbs has been largely a response to refrigerating climates, it must be apparent that, given the progenitor-stocks, herbs would had a phenomenal epoch of development during the Permo-Carboniferous glaciation.

[1] "De nos jours, les Smilacées sont mêlées aux Cycadées dans l'Afrique australe, la Nouvelle-Hollande et l'Inde. Existaient-elles déjà dans l'hémisphère austral, au Japon, au Mexique, etc., quand les terrains jurassiques se formaient en Europe? C'est extrêmement probable; malheureusement on connait peu de fossiles de ces pays lointains, et les géologues ne sont guère en état de certifier ce qui se passait dans une même période d'années à des distances aussi grandes."—A. DC. Mon. Phan. i. 35 (1878).

[2] For summary of literature and pertinent discussion see Arber, Agnes, *The Tree Habit in Angiosperms: its Origin and Meaning*, New Phyt. xxvii. 71–84 (1929).

[3] Engler, Natürl. Pflanzenf. ed 2, xiv^a. 138–145 (1926).

[4] Map 21 reproduced, with permission, from p. 91 of Coleman, Ice Ages Recent and Ancient (New York. Macmillan).

Gondwana was, after all, only a hypothetical land. Originally reconstructed and subsequently greatly extended to account for the disrupted localities of now fossil species, it furnishes a sort of explanation of early tropical dispersal. But, at this very day, hundreds of living groups of Angiosperms (as well as many groups of Pteridophytes) have a "Gondwana" or relic pantropical range. Nevertheless, there is now no circum-tropical connection, such as is generally assumed for Permian time, between these areas of living plants; consequently, the hypothetical status of Gondwana becomes strikingly accentuated.

Leaving these purely theoretical realms and returning to better demonstrated and, consequently, firmer geological and paleontological grounds, we are at least justified in looking upon the present Atlantic North American representatives of prevailingly tropical groups as lineal descendents of plants which reached eastern North America out of the North at a time, during the Mesozoic and perhaps early Cenozoic, when the ancient rock-floor which now constitutes the Appalachian Upland was peneplained or near sea-level. With the Cretaceous seas (see MAP 20) occupying the north-and-south center of the present continent and its southern and southeastern margin and the Tertiary seas later invading much of the southern and eastern portion of the same area, the only section of present eastern continental North America then continuously accessible to these plants was the ancient baseleveled Appalachian region with the Laurentian shield to the north and northwest.[1] Then, as the later uplifting of the once peneplained Appalachian region progressed, making halts at intervals through Tertiary time, with the consequent deep dissection of the extensive plateau and its inevitable conversion from a low Cretaceous plain with retarded drainage into a vast upland mesophytic area, ready for occupation by the abundant mesophytic types of the climax forest which could now freely mingle between Asia, northwestern America, eastern North America and Europe, the members of the tropical and subtropical groups (and with them many endemic groups) represented in eastern North America were largely forced (by drainage of the area and by invasion by the hoard of actively colonizing mesophytic types) to abandon their once congenial but now un-

[1] In this connection, the absence from Pacific North America of the hundreds of tropical and subtropical groups which linger on the Atlantic Coastal Plain is significant; during the Cretaceous eastern and western North America were completely isolated from each other (see MAP 20).

congenial haunts on the Appalachian area and to move out to the newly available xerophytic and hydrophytic habitats, chiefly on the Coastal Plain (though in some instances west and northwest of the Appalachian axis), where the acid savannahs, bogs, shallow pools and dry sands supply the ecological conditions in which these descendents of Cretaceous and early Tertiary hydrophytes and xerophytes can still survive.

In 1897, Dr. T. H. Kearney, directing attention to "*The Pine-barren Flora in the East Tennessee Mountains,*"[1] said: "One would hardly expect to find a large proportion of this flat country flora hidden among the high ridges of the Alleghanies; yet this is unmistakably the case. Especially along the picturesque French Broad river, . . . there is a notable incursion of plants usually considered typical of the coastal plain," and, after enumerating several such species, Kearney continued: "What are we to infer from the presence of these austro-riparian plants among the flora of northern origin that chiefly covers these mountains? Possibly they are the advance-guard of an invading army. Much more probably, however, they are the lingering survivals of a more southern flora, once widely distributed over the southern Appalachian region." Three years later, developing the subject more fully and interpreting the migration to the Coastal Plain as a response to Pleistocene cold, Kearney[2] suggested that "it may be conceived that while some individuals of each hypothetical Pliocene ancestral species maintained themselves in well-sheltered situations and were not forced [by Pleistocene cold] to a change of abode,[3] others escaped the changing environment by a gradual retreat into the warmer lowlands. The individuals which remained in the mountains were the direct ancestors of the present Appalachian species; while those which migrated and later accustomed themselves

[1] Kearney, Plant World, i. 33–35 (1897).

[2] Kearney, *The Lower Austral Element in the Flora of the Southern Appalachian Region*, Science, ser. 2, xii. 830–842 (1900), especially p. 839.

[3] The effect upon vegetation of ice-sheets hundreds of miles away was probably not so great as was formerly supposed. Witness the occurrence today of splendid forests *on* the glaciers of Alaska; and the occurrence at the ice-free margin of otherwise ice-capped Greenland of such plants of sea-level in the eastern United States as *Woodsia ilvensis, Cystopteris fragilis, Equisetum sylvaticum, E. hiemale, Deschampsia flexuosa, Carex brunnescens, Streptopus amplexifolius, Corallorrhiza trifida, Stellaria borealis, Ranunculus Cymbalaria, R. reptans, Coptis groenlandica, Potentilla palustris, Viola Selkirkii, Epilobium angustifolium, Cornus canadensis, Pyrola secunda, Andromeda glaucophylla, Vaccinium Oxycoccus, Menyanthes trifoliata, Utricularia intermedia* and *Linnaea borealis*, var. *americana;* or the occurrence on tablelands of Newfoundland or Gaspé of members of chiefly tropical groups almost side-by-side with typical plants of Ellesmereland and Melville Island.

in the Coastal Plain . . . gave rise to the Austro-riparian species that attract our attention today because of their close resemblance to Appalachian forms." In 1904 the late Professor Harshberger[1] suggested a similar derivation of some of the endemic North American plants of the Coastal Plain from the crests of the Alleghenies. Somewhat later, Dr. Witmer Stone stated that "The flora at the top of Meadow Mountain, the summit of the Alleghenies [in Garrett County, Maryland], . . . was very much as in the pine barrens of New Jersey, and is quite likely a remnant of an early primitive flora such as we have there."[2] In 1924 Dr. John K. Small expressed the same view. The relic-genus *Narthecium* (or *Abama*) has one wide-ranging species in Europe, one or two highly localized species in the eastern Mediterranean region, one in Japan, one in California and Oregon; and it has long been of great local interest in eastern America through *N. americanum* Ker., a famously rare plant of the very heart of the New Jersey Pine Barrens. But in 1919 a species closely related to *N. americanum* was discovered at a single station in the mountains of North Carolina. In describing the mountain plant as *Abama montana*, Small said: "It is not surprising that a bog-asphodel should come to light in the mountains of North Carolina, as several kinds of plants otherwise known only in the pine-barrens of the middle Atlantic Coastal Plain also grow in the Appalachians. . . . It is scarce, evidently rare, and may be on the verge of extinction. It may be that in this species we have one of the progenitors of the *Abama* of the Coastal Plain, for the high mountain region was the reservoir whence many of our Coastal Plain plants were derived."[3]

The derivation of much of the flora of the youthful Coastal Plain of the United States from the ancient Appalachian Upland, which in the Cretaceous itself had a coastal-plain status, is strongly supported by the very striking condition in the Antillean and Mexican regions. As shown by Schuchert[4] (MAPS 22–27), portions of the Greater Antilles (Cuba, Haiti, Jamaica, Porto Rico, etc.) have been in continuous existence at least since the Lower Cretaceous and much of the time connected with the Central American and Mexican tablelands; but the Bahama Islands did not rise above the sea until the Miocene,

[1] Harshberger, Proc. Acad. Nat. Sci. Phila. 1904: 607.
[2] Stone, as reported in Bartonia, No. 5: 16 (1912).
[3] Small, Torreya, xxiv. 86 (1924).
[4] Schuchert, *Geological History of the Antillean Region*, Bull. Geol. Soc. Am. xl. 337–360 (1929), from which my maps 22–27 are photographed.

while all but the base of the Peninsula of Yucatan is even younger. It is, therefore, significant, when we check the living floras of the Bahamas[1] and of Yucatan,[2] to find that on these very youthful areas, which are far isolated from more ancient upland centers, there are no species of *Schizaea* (MAP 9), the *Haemadoraceae* (MAP 10), the *Xyridaceae* (MAP 12) and *Lycopodiaceae* (see MAP 17); but that on the older Greater Antilles and the old Mexican or Central American Plateaus or their margins these groups of the young Coastal Plain of the United States are all represented. Ancient *Diospyros* (MAP 14), also, is on the Greater Antilles but, although locally present in Yucatan, it is absent, as a native, from the Bahamas. Many other tropical or austral groups which today have a northern remnant persisting on the young Atlantic Coastal Plain of the United States and on the ancient Greater Antilles and the equally ancient Mexican or Central American Plateaus or at their margins, are absent, likewise, from the young Bahamas and from still younger Yucatan (except occasionally as cultivated species or as relics of cultivation): such groups as the *Eriocaulaceae*, in Mexico up to 3355 m. (11,000 ft.), the *Marantaceae*, up to 915 m. (3000 ft.), the *Burmanniaceae* (MAP 18), up to 1675 m. (5500 ft.), *Bochmeria*, up to 1585 m. (5200 ft.), *Clitoria*, up to 2135 m. (7000 ft.), *Rotala*, up to 1525 m. (5000 ft.), *Myriophyllum* § *Tessaronia*, up to 1740 m. (5700 ft.) and *Dyschoriste*, up to 2400 m. (8000 ft.); while *Psilocarya* occurs on the Greater Antilles but not in Mexico and *Litsea* in Mexico ascends to 3050 m. (10,000 ft.). Similarly, on the Mexican Plateau we find representatives of *Xyris* at 1830 m. (6000 ft.) and of *Schizaea* at 1200 m. (3925 ft.).

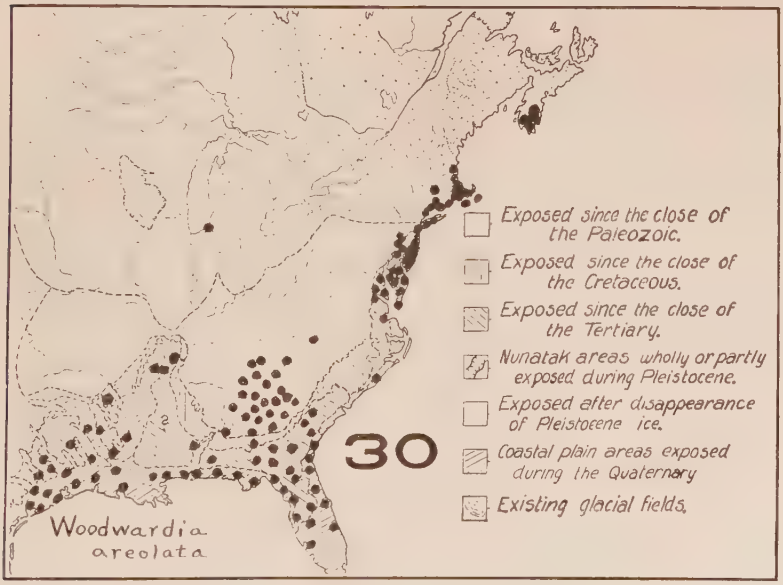
The always interesting genus *Drosera* (MAP 28),[3] with three circumboreal species and another (*D. linearis* Goldie) confined to boreal America, has most of its living species concentrated in the Southern Hemisphere and in southern Asia, with a few related species on the Greater Antilles, on the Coastal Plain of the United States and in Central America; but the genus is unknown from either Yucatan or the Bahamas. The unique *D. filiformis* Raf., however, differs from all other American species in its hardened bulbiform woolly base, its linear-filiform and very prolonged (up to 6 dm.) leaves without elon-

[1] See Britton & Millspaugh, The Bahama Flora (1920).

[2] See Standley, *Flora of Yucatan*, Field Mus. Publ. 279—Bot. Ser. iii. no. 3 (1930), which has come to hand while this paper is going to press.

[3] The map is largely copied from that of Diels in Engler, Pflanzenr. iv [112], supplemented by material in the Gray Herbarium. The North American range is altered to accord with the specimens and citations covering this area.

Map 28, Geographic Range of Drosera, the boreal Species indicated by Stippling, and of Drosophyllum (in ellipse).



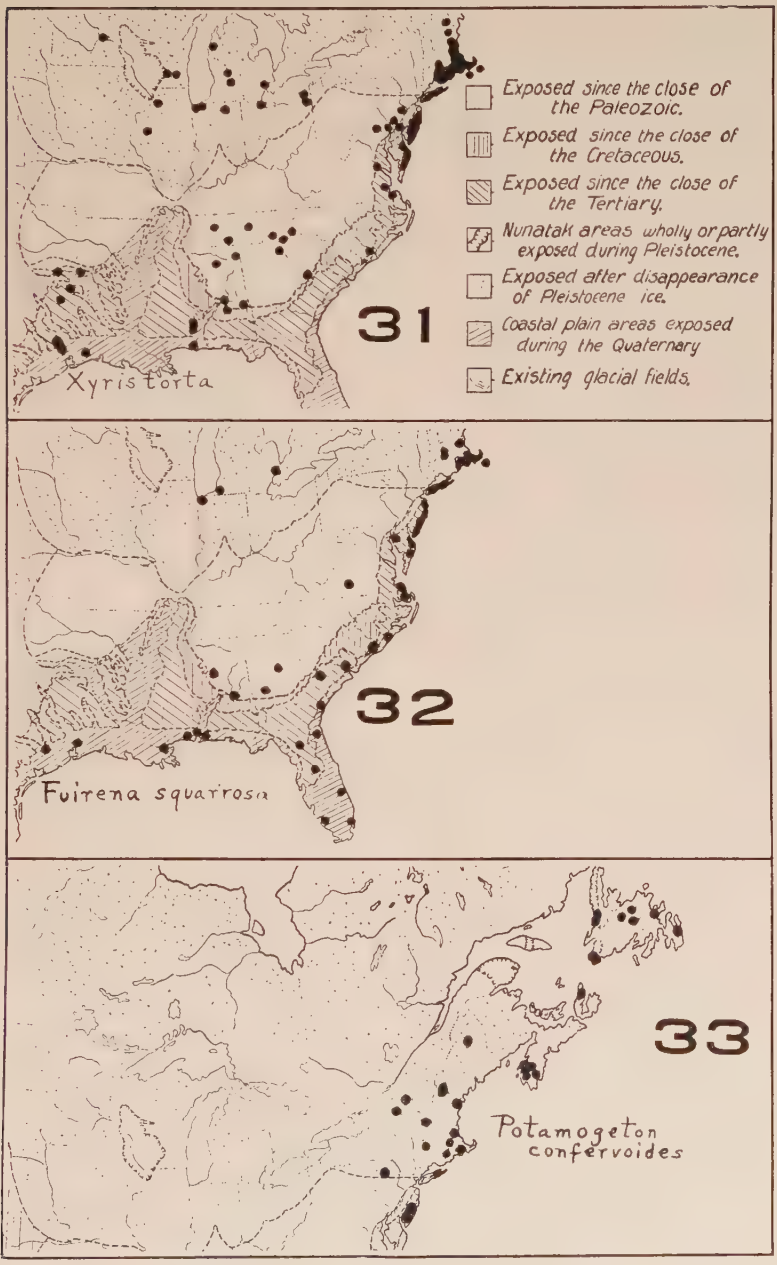
Map 29, Geographic Range of Drosera filiformis (upper and lower black areas) and of Dionaea (middle black area); 30, of Woodwardia areolata (an additional station should be recorded, at the southwestern end of Lake Erie).

gate petiole, its large purple petals and its seeds; it is far more closely related to some of the Indian, Malayan and Australian species than to any of the broad-leaved, long-petioled and white-flowered species (of § *Rossolis*) with which it grows. It is restricted to two wholly disrupted areas of the Coastal Plain (see MAP 29) and its present distribution is best explained as a result of migration in two directions off the now uplifted Appalachian Upland. Outside the now essentially austral and tropical genus *Drosera* the family has two monotypes: *Drosophyllum lusitanicum* L. (see MAP 28) of the ancient Iberian Tableland and adjacent Morocco and *Dionaea muscipula* Ellis (see MAP 29) of the Cretaceous (hardly Tertiary or Quaternary) Coastal Plain of the Carolinas.[1] The antiquity of the insectivorous *Droseraceae*, therefore, can scarcely be doubted.

Not only, as we have seen, do the tropical groups represented on the Atlantic Coastal Plain of the United States have representatives on the high tablelands of the Appalachian Mountains, on the older of the Antilles and on the high plateaus of Mexico or of Central America; they are also well represented at low levels west and northwest of the Appalachian axis, particularly in the upper Mississippi Valley, and about the Great Lakes where the sands and peats of Pleistocene or later origin offer them peculiarly attractive habitats. Their migration out from the now elevated Appalachian area to the Coastal Plain on one side, to the region of the Great Lakes on the other, is clearly indicated by *Woodwardia areolata* (L.) Moore (MAP 30), a characteristic fern of the Coastal Plain but also found on the tablelands of the southern Appalachians at 3000 ft. (915 m.), and otherwise known only in northwestern Ohio and in southwestern Michigan.

This movement out from the Appalachian center is even better displayed by the very distinct, bulbous *Xyris torta* Sm. (MAP 31), a common species of the Coastal Plain sands, also at 2000–4000 ft. (610–1220 m.) on the high silicious tablelands from North Carolina and Tennessee southward, and with a rather extensive area about the Great Lakes. In these cases (and scores of others which might be cited) migration from the ancient Appalachian region is a reasonable explanation of the present segregations. In some other cases we do not now (or yet) know any existing stations high on the Appalachians but it is fair to assume that during the baseleveled Cretaceous stage of this area they must have there existed; and it is reasonable to be-

[1] For all known stations see Coker, *The Distribution of Venus's Fly Trap (Dionaea muscipula)*, Journ. Elisha Mitchell Sci. Soc. xliii. 221 (1928).



Map 31, Geographic Range of Xyris torta; 32, of Fuirena squarrosa; 33, of Potamogeton confervoides.

lieve that, to the already surprisingly large number of relic-colonies of tropical types known on the mountains of the Carolinas and Tennessee, stations of members of these other groups may soon be added. *Potamogeton*, sub § *Javanici* (map 13), not yet known either on the Appalachian Upland or on the true Coastal Plain, is decidedly an exception. Much more typical is *Fuirena squarrosa* Michx. (map 32), characteristic of Coastal Plain sands, with a slight overlap on the ancient Piedmont area, but unknown from the high tablelands, and isolated on the sands of southern Michigan and northern Indiana. The *Burmanniaceae* (map 18) yield an even more striking instance. The family is widespread in tropical and subtropical regions but, like many other groups, it has a slight extension northward in eastern Asia and another around the Gulf and Atlantic Coastal Plains of the United States. North of Virginia the family is unknown, save for the extraordinary little species of prairies at Chicago, *Thismia americana* N. E. Pfeiffer.[1] This, as noteworthy a plant as is known in the Great Lake area, is the more remarkable since it belongs to a small subfamily otherwise confined to the Tropics, chiefly of the Old World.

The cases I have presented are merely a few illustrations but, without further enumeration or further analysis, enough have been presented to make it clear that, to a large extent the tropical groups which today have a representation on the Atlantic Coastal Plain of the United States or about the Great Lakes are also found persisting (often as rare relics) on the high tablelands of the Mexican Plateau as well as on the tablelands of the Appalachian Mountains or at other spots back of and older than the outer Coastal Plain. I am aware that, in looking upon the members of these and other primitive groups which now occur upon or among the mountains of north-eastern Pennsylvania, northern New York and western and northern New England as preglacial relics there, I am not in full accord with orthodox Pleistocene geology, which asks us to believe that the late ice-sheets so vigorously overrode these mountains as to denude them of all life. The parallelism is so definite, however, between these Coastal Plain species having representatives on the elevated tablelands of the more southern and quite unglaciated Appalachians, as well as on the Central American, Mexican and Antillean tablelands, and their occurrence on the supposedly denuded mountains farther north, that the botanist, at least, is forced to believe that the Pleistocene de-

[1] Pfeiffer, *Morphology of Thismia americana*, Bot. Gaz. lvii. 122–134 (1914).

struction of plants on the high mountains of New England, New York and northeastern Pennsylvania has been vastly overestimated. It is far more logical to look upon the very primitive *Potamogeton confervoides* (MAP 33), an aquatic with plump fruits not adapted for flying, as a preglacial relic on the high mountains of northern and western New England, on the Adirondacks and on the Pocono Plateau (as well as on the unglaciated or but slightly glaciated tablelands of Newfoundland and of Cape Breton), than to picture it as making a post-Wisconsin leap from the coastal pools to the highest mountain-masses far to the northwest and north and successfully finding welcoming pools on them all, but not landing in the thousands of intermediate lowland ponds. *P. confervoides*, one of the most primitive members of the worldwide subgenus *Eupotamogeton*, is so rare that only a few botanists have ever seen it growing. If any lowland pondweed were in post-Wisconsin time to do the improbable and invade the elevated mountain-pools from sea-level, it would less unreasonably be a common or, in the region, essentially ubiquitous and less primitive species (also of peaty depressions and pools), such as *P. pusillus* L., *P. Spirillus* Tuckerm., *P. epihydrus* Raf.[1] and *P. gramineus* L.; but these almost weed-like species of all pools at low levels, north, south, east and west, have not invaded the mountain-ponds of New England, New York and Pennsylvania, where the primitive and excessively rare Coastal Plain *P. confervoides* and its Coastal Plain congener, *P. Oakesianus* Robbins, alone represent the genus. Near the White Mountain stations of *P. confervoides* occur two endemic alpine xerophytes: *Potentilla Robbinsiana* Oakes, nearest related to the Siberian *P. elegans* C. & S.; and *Geum Peckii* Pursh, the isolated representative of *G. calthifolium* Mertens of the North Pacific and Bering Sea region. Obviously these two endemic neighbors of the Coastal Plain *Potamogeton confervoides* on the White Mountains have not originated there in post-Wisconsin time.

If this general reasoning is correct, that the Coastal Plain plants of the eastern United States before occupying the youthful Coastal Plain had had direct progenitors on the Cretaceous peneplain which, through Tertiary uplifts, has again become the Appalachian Moun-

[1] Although not found in the high subalpine ponds of New England and New York, *Potamogeton epihydrus* is, surely, to be sought there. On the great tableland of the Table-top Range in Gaspé, which Coleman and Alcock independently conclude "escaped the erosion of the continental ice sheets," it occurs in the pools along with *Myriophyllum Farwellii* Morong, the most northern representative of the tropical and Coastal Plain *Myriophyllum* § *Tessaronia*.

tains, it follows that these Coastal Plain groups are of as ancient ancestry as any angiosperms now living in eastern North America. It is, therefore, particularly noteworthy that in world-wide groups their representatives are invariably regarded by monographers as wholly differentiated specifically from their relatives now living in Africa, tropical India and Australia.

When we turn northward to the physiographically very youthful soils (or lack of soils) which have resulted from the Pleistocene glaciation, much of the vast area of eastern Canada and the northernmost States, a region in which the plant-population is, in some places, just moving in to occupy the newly available territory, we find a great assemblage of dominantly boreal (or extreme austral) genera: *Sparganium*, *Festuca*, *Glyceria*, *Agropyron*, *Calamagrostis*, *Eriophorum*, *Carex*, *Juncus*, *Salix*, *Alnus*, *Betula*, *Sorbus*, *Rubus*, *Fragaria*, *Potentilla*, *Rosa*, *Lathyrus*, *Epilobium*, *Pyrola* and hundreds of others. Although many stable species in this flora, like *Sparganium minimum* Fries, *Potamogeton filiformis* Pers., *P. obtusifolius* Mert. & Koch, *P. praelongus* Wulfen, *Triglochin palustris* L. and *maritima* L., *Cinna latifolia* (Trev.) Griseb., *Eriophorum gracile* Koch, *Caltha palustris* L., *Pyrola minor* L. and *Lysimachia thyrsiflora* L., are regularly regarded as identical with plants of Eurasia, others, like *Scheuchzeria palustris* L.[1] and *Menyanthes trifoliata* L.,[2] in eastern America are sufficiently different from the Eurasian plants in size of flower or fruit as to receive varietal designations; but no one has seriously proposed to treat them as different species. And when we get into heteromorphic tangles like *Festuca rubra*, the *Poa pratensis* jumble, *Agropyron repens*, *Calamagrostis canadensis* (including *Langsdorfi*), the *Carex vesicaria* morass, *Juncus effusus*, the *Salix glauca* complex, *Alnus incana*, the *Betula alba* forest, *Cerastium arvense*, *Sorbus*, *Rubus idaeus*, and a full hundred other always perplexing mazes, common experience on both sides of the Atlantic is sufficient to indicate the utter lack in these groups of the clear specific differentiations which every systematist looks for but in these plants fails to find.

The key-note in this youthful flora of the vast Canadian region, mostly available for plant-occupation only during the last few thousand years, is, then, the essential lack of fundamental specific segregation from the European representatives of these plants. This is in marked contrast with the condition shown in the amphigean

[1] See Fernald, Rhodora, xxv. 178 (1923).
[2] See Fernald, Rhodora, xxxi 195 (1929).

genera now characteristic of the ancient Appalachian Upland and with the sharp specific differentiation of the Coastal Plain species from their allies in Africa, tropical Asia and Australia. Whether we derive the disrupted colonies of the tropical groups out of the widespread boreal flora of the Cretaceous and early Tertiary, which seems to me the logical deduction, or whether we prefer to picture them as having spread across a hypothetical trans-Atlantic land, it is clear that long after the tropical floras had become geographically separated the northern lands still maintained a broad connection. Many geologists have postulated a late Tertiary and Pleistocene uplift of the Arctic lands. Thus, Mecking,[1] following Suess, says of the Arctic: "At the end of the Tertiary began an uplift which continued into the Glacial Period. At the climax of the latter there followed a general sinking, which, by filling the valleys and troughs, created the sounds and then gave way to a newer uplift which still continues"; and Simmons, summarizing the various studies of former continuity of Arctic lands, concludes: "That the northern parts [of North America] . . . were lifted considerably above their previous level, cannot be doubted . . . most authors are inclined to refer the beginning of the rise . . . to the last part of the tertiary era."[2] The amount of this late Tertiary and early Pleistocene uplift has generally been estimated at 2000–3000 feet (600–900 meters); and study of Dr. Nansen's bathymetric map[3] of the Arctic Basin shows that an elevation of 2000 feet (600 meters) would today unite northwestern America and Asia and would connect northeastern America by two routes with Greenland, thence via Iceland with Scotland and Scandinavia. It is, then, quite clear that in late Tertiary, and probably in early Pleistocene time, the northern plants had essentially free routes for interchange between Eurasia and North America. Consequently, sharp specific differentiation in the comparatively youthful plants of amphigean relationship which are chiefly restricted to recently glaciated northern Europe and recently glaciated northern America is the exception rather than the rule.

Time does not permit my now specially discussing the outstanding

[1] Mecking, *The Polar Regions: a Regional Geography*, Geogr. Polar Reg., Am. Geogr. Soc., Sp. Pub. no. 8: 220 (1928).

[2] Simmons, *A Survey of the Phytogeography of the Arctic American Archipelago*, Lunds Univ. Årsskrift. n. f. Afd. 2, Bd. 9, Nr. 19: 152 (1913).

[3] Bathymetric Map of the Arctic Basin in Nansen, *The Oceanographic Problems of the still unknown Arctic Regions*, in Problems of Polar Research, Am. Geogr. Soc., Sp. Publ. no. 7, t. 1 (1928).

features of certain other floras in eastern America, like the high degree of relic-endemism on the nunatak areas, a topic already discussed by me in other papers[1] (190 rare and localized endemics already known, and 160 others with relic-colonies isolated by 1500–4500 miles from other colonies of the species), or the multiplicity of intergradient forms[2] of *Panicum*, *Salix*, *Amelanchier*, *Crataegus*, *Rubus*, *Vaccinium* (§ *Cyanococcus*) and *Aster* and the dominance of more than 1000 aggressive species introduced from Europe during the last three centuries on the clearings made by the white man, the youngest spots of all. From what I have been able to present, however, certain deductions, by way of summary, seem justified:

1. The characteristic flora of the present southern Appalachian Upland, made up largely of groups which were cosmopolitan in the Mesozoic or early Cenozoic but now reduced to geographically segregated remnants in the Northern Hemisphere, is obviously ancient and its species are usually (but not always) clearly differentiated from those of the same genera in eastern and central Asia or in southeastern Europe.

2. The Coastal Plain flora of Atlantic North America is distinguished by the abundance of tropical groups represented. Although these plants now chiefly occupy open silicious, peaty and aquatic habitats in comparatively youthful regions of eastern North America, it is probable that they or their progenitors formerly existed on the area of the ancient Appalachian Upland, especially in the Cretaceous, when that primitive region of the continent was baseleveled and reduced essentially to sea-level and at the time when the tropical groups of today were widespread in the North. Then, with the Tertiary uplift of the Appalachian region and its final conversion into a vast well-drained mesophytic area available to the groups which now constitute the climax forests of the Appalachian Upland, the Cretaceous xerophytes and hydrophytes which had previously occupied the ground gradually moved out to the newly available and for them more congenial Coastal Plain and similar habitats to the west and northwest. These species of the Coastal Plain, whose direct progenitors were probably segregated geographically from their

[1] For discussion see Fernald, *Isolation and Endemism in Northeastern America*, Am. Journ. Bot. xi. 564 (1924); *Persistence of Plants in Unglaciated Areas of Boreal America*, Mem. Am. Acad. xv. 242–244 (1925); *Some Relationships of the Floras of the Northern Hemisphere*, Proc. Internat. Congr. Pl. Sci. ii. 1493, 1494 (1929).

[2] For discussion see Fernald, *The Antiquity and Dispersal of Vascular Plants*, Quart. Rev. Biol. i. 236–238 (1926).

African, Indian and Australian allies during the Cretaceous or the early Tertiary, are thoroughly differentiated from the Old World species.

3. The nunatak areas, the scattered unglaciated or only slightly glaciated spots within the region of more widespread glaciation, are distinguished by a high degree of relic-endemism.

4. The dominant groups of the region of northeastern America only lately freed from Pleistocene ice are largely those of recently glaciated northern Europe. These northern lands have been so recently segregated geographically that until geologically recent time there has been free interchange in the floras; and in the ecologically youthful Canadian and northern European regions identity of species in the amphigean genera is so general as to become the rule.

5. The recently cleared lands, like the recently glaciated areas and the Quaternary sands, are also characterized by a multiplicity of variable and often intricately intergrading and hybridizing forms, as well as by the aggressive dominance of unchanged species introduced within three centuries from the youthful flora of Europe.

Some of the points I have discussed are possibly new, though many of them are familiar and very old-fashioned doctrines; but since familiarity so often breeds contempt and the latest doctrines are so frequently supposed to be the best, it may not be amiss to call attention anew to the overwhelming evidence of the soundness of some of the older deductions.

A White-flowered Form of Aster amethystinus.—Two stations made up of plants transplanted from the type colony of *A. amethystinus* f. *leucerythros*[1] in 1924 and 1925, have several times apparently developed pink-flowered seedlings. This year one of the stations produced a white-flowered seedling.

Aster amethystinus Nutt., f. **leucos**, n. f. ligulis albis.—Massachusetts: Worcester, September 24, 1930, *E. W. Bemis* (type in Gray Herbarium).—Earl W. Bemis, Worcester, Massachusetts.

Carex Bebbii in eastern Massachusetts.—On 15 July 1930 I collected in a meadow in Stoughton, Massachusetts, specimens which have been identified by Prof M. L. Fernald as *Carex Bebbii*

[1] Rhodora **32**: 3. 1930.

Olney. The presence of this sedge in eastern Massachusetts has not generally been recognized, and the species is not listed in the *Flora of the Boston District* published some years since in Rhodora. In the last edition of Gray's Manual it is assigned a range from Newfoundland south to western Massachusetts and New York, and westward. In the second edition of Britton and Brown's Illustrated Flora the range is extended south to New Jersey. Its presence as a scattered plant at other places in the eastern part of Massachusetts is shown by specimens in the herbarium of the New England Botanical Club collected in a swamp at Chilmark, Marthas Vineyard, by Sydney Harris on 29 July 1894, and beside a railroad at West Manchester by F. Tracy Hubbard on 30 June 1911.—S. F. Blake, Bureau of Plant Industry, Washington, D. C.

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Photo. by H. M. Raup.

Potamogeton confervoides (left) and P. pectinatus (right) × ½.